

Enhancing Water Use Efficiency and Effective Use of Water as A Potential Strategy to Develop Rice Cultivars Suitable for Semi-Irrigated Aerobic Cultivation

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Abstract

Semi-irrigated aerobic rice is a potential rice cultivation strategy to substantially save irrigation water even up to 40-60%. However, under these conditions rice crop experiences high vapor pressure deficit (VPD) and between irrigations moderate moisture stress leading to decline in plant water status thus affecting plant growth and spikelet fertility. This necessitates need to improve plant traits associated with water relations like water mining, water use efficiency (WUE) and water retention besides cellular level tolerance. An effective use of water is considered as a preferred target for crop yield improvement than water use efficiency under water limited conditions. We provide evidence from our study that indicates WUE as a still relevant trait across genotypes with adequate canopy cover and total transpiration (total T). The importance of identifying genotypes with higher WUE achieved by improving mesophyll efficiency is discussed. The importance of waxes to maintain lower canopy temperature and superior water relations implicate the relevance of this trait as well. In rice accessions, we have found an inverse relationship between roots (and hence total T) and WUE signifying the need to breed for both the traits. Our study provides proof of concept that introgressing root traits with higher WUE will increase crop growth rate (CGR) and productivity in semi-aerobic ecosystem. One of the trait introgression lines when grown under aerobic conditions showed superior performance.

Keywords: Semi-irrigated rice, aerobic rice, water use efficiency, root traits

Introduction

With the looming crisis for water due to erratic monsoon seasons and increased demands, water availability for irrigation is constantly declining and resulting in a severe constraint on crop productivity. Conventional rice cultivation under puddle conditions is the most water intensive practice. Thus, attempts to save water from rice fields deserve the most emphasis. Among the several agronomic methods available, the semi-irrigated aerobic cultivation with the less frequent irrigations significantly reduces the water requirement and is likely to save up to 60% of irrigation water. However, a concomitant reduction in yield must be avoided if the water saving advantages of semi-irrigated aerobic cultivation is to be fully exploited. This necessitates the design and development of new rice cultivars that are resilient to the semi-irrigated aerobic cultivation. In conventional puddle conditions, rice plants are normally exposed to high relative humidity in soil that is constantly at saturated conditions. The high RH (and hence a low VPD) leads to reduced

transpirational losses and hence the plants can maintain positive turgor. On the contrary, the aerobic fields are characterized by high VPD which results in greater transpiration and transient loss of leaf turgor.

Further, low RH induced stomatal closure can affect carbon gain. Under low RH (high VPD), when water uptake does not match the transpirational demand, a transient decrease in the plant water status severely affects the CGR and significantly reduces the spikelet fertility. Under these conditions, acquisition of specific nutrients is yet another constraint that limits productivity. From this context, improving the water relations of the rice plants when grown under the semi-irrigated aerobic conditions is very crucial for sustaining productivity while saving irrigation water. Thus, genetic enhancement of rice genotypes to evolve suitable cultivars with improved water mining, water use efficiency, and conservation has phenomenal relevance for adaptation and improved productivity.

Relevance of water use efficiency (WUE) as a potential drought adaptive trait

Water use efficiency (WUE) is an extremely important component of water productivity. With an increasing scarcity of water for irrigation, enhancing the water productivity has the greatest relevance. WUE can be defined at several levels. For instance agronomically, WUE is the yield of a crop to the amount water used as irrigation. However, physiologically, this term has more precise definitions: at a whole plant level, it is the ratio of the biomass produced to the total water transpired from the plant canopy over a specific period of time and expressed as grams per kilogram; and at a single leaf level, WUE is the μmol s of CO_2 fixed per mol of water transpired.

Both photosynthesis and transpiration are often considered as diffusive processes where the substrate CO_2 diffuses into the leaf while water vapor diffuses out of the leaf. As WUE is a ratio of these processes, factors that control of diffusion of these gases would determine the differences in WUE. Thus, it would be appropriate to improve the carbon gain per unit transpiration for enhancing growth and productivity.

Stomatal conductance controls the diffusion of both CO_2 and water vapor and hence is the most important determinant of this gas exchange. At a given stomatal conductance, however, the rates of diffusion of these gases entirely depend on their diffusion gradients. While CO_2 concentration difference between the leaf and the atmosphere is the driving force for CO_2 diffusion, the vapour pressure difference (VPD) between the leaf and atmospheric air is the major determinant of evaporation of water during transpiration. It is generally observed that VPD between leaf and air is at least a 1000 times higher than the CO_2 concentration gradient. Thus transpiration rate will be significantly higher than photosynthetic rate resulting in only a few grams of biomass (1 to 2 g) accumulated for every kilogram of water transpired or at a single leaf level, a few μmol s of CO_2 fixed for every mole of water transpired. Thus, increasing carbon gain for unit transpiration has tremendous advantage and is hence essential for achieving higher water productivity.

Having realized the importance of WUE, several attempts were made to assess the genetic variability in this trait. Considerable genetic variability in the diffusive conductance for CO_2 and water vapor was observed which in turn resulted in the existence of a significant genetic variability in WUE (Table 1). Efforts in assessing the genetic variability in carbon gain per unit transpiration (WUE) was given the greatest impetus with the discovery that plants discriminate against the heavy isotope of carbon (^{13}C) during photosynthesis.

Table 1. Genetic and species variation in WUE in a few important crop plants

Species	Mean	Range
Sunflower	2.80	2.10 – 3.50
Cowpea	2.64	1.98 – 3.28
Groundnut	2.35	1.81 – 3.00
Rice	2.52	0.54 – 3.58

This isotope discrimination ($\Delta^{13}\text{C}$) is linked with WUE on a time integrated scale (O'Leary 1981; Farquhar and Richards 1984; Farquhar et al 1989).

With the establishment of the theory linking WUE and $\Delta^{13}\text{C}$ and because of the high throughput measuring abilities for isotope ratios, tremendous progress was made in assessing the genetic variability in WUE using this surrogate (Sheshshayee et al 2003; Condon et al 2004; Impa et al 2005). In many germplasm accessions of several crop species including rice, we observed significant genetic variability in $\Delta^{13}\text{C}$ (Table 2). Several other research groups demonstrated the existence of remarkable variation in WUE in several crop species (see references in Sheshshayee et al 2003).

Analysis of the higher productivity of C_4 plants led to the understanding that they do so because of a significantly higher WUE and hence the growth rate at any given input of water was quite high in C_4 species. Information accruing in the literature clearly demonstrates the relevance WUE as an extremely relevant trait for sustaining crop growth, especially under water limited conditions. Methodological advances have paved way for the rapid determination on WUE both on a single leaf level as well as on a time averaged scale which revealed a significant genetic variability in this trait. Relevance and the amenability for phenotyping for WUE in large number of lines using high throughput approaches stimulated the interests among breeders to improve WUE in C_3 species to achieve improved growth rates.

The most extensively accepted growth and yield model is that of John Passioura where WUE was as an important component that determined growth and productivity (Passioura 1986).

Table 2. Genetic variability in $\Delta^{13}\text{C}$ among diverse germplasm of different crop species

Species	Range in $\Delta^{13}\text{C}$ (‰)
Groundnut varieties (54)	17.86 - 20.18
Groundnut germplasm (266)	18.26 - 21.97
Rice germplasm (230)	18.15 – 22.79
Rice mapping population (100)	19.21 - 22.55
Mulberry germplasm (293)	17.47 – 24.38

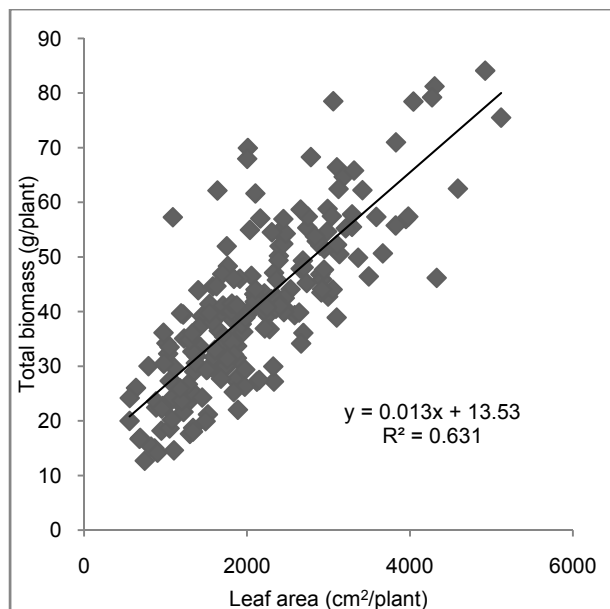


Figure 1. Relationship between total biomass and total plant leaf area among diverse rice germplasm accessions

This model formed the framework for most of the breeding programs that were initiated to improve WUE (Richards et al 2000; 2002, Condon et al 2004). However, selection for high WUE under water limited condition often resulted in a decrease in total biomass (Blum 2009, 2011). Further, inconsistent relationship between WUE and total biomass recorded in diverse experiments dampened the initial enthusiasm to breed for improved WUE and the emphasis shifted towards improving effective use of water which is determined by total transpiration (Blum 2009). Being an important component of the Passioura yield model, the reasons for the decreased biomass production while selecting for higher WUE must be viewed carefully and approaches need to be developed to circumvent this situation.

Under conditions when water loss is greater than water uptake, a situation that generally occurs during water deficit or when the root system is not well developed, plants maximize WUE through a reduction in transpiration rate. This results in the reduction in tissue water status which besides reducing stomatal conductance, directly affects leaf expansion and hence reduces leaf area. Thus, water limited conditions affect two important factors, viz, leaf area and stomatal conductance which together significantly reduce canopy photosynthesis.

Similarly, leaf area and transpiration rate per unit leaf area determine total water use. Therefore, selection for higher WUE indirectly results in a substantial reduction in total transpiration. Since this decrease in total

transpiration is generally linked to reduced leaf area and/or transpiration rate, a negative relationship between total biomass accumulation and WUE is normally encountered.

In this background, it can be visualized that WUE contributes to total biomass accumulation only when increase in WUE does not affect total transpiration. Stress induced reduction in leaf area in principle results in decreased biomass accumulation despite an increase in WUE. In our experiments with large number of rice germplasm accessions, the differences in total biomass were strongly dependent on leaf area (Fig. 1) and total transpiration (Fig. 2). Since the phenotypic variance of leaf area and total transpiration are larger than WUE, leaf area and total transpiration exert greater influence on growth rates than WUE.

Therefore, crop improvement programs must adopt a sequential approach. It is imperative that the initial selection be made for higher canopy cover or total transpiration.

Subsequent selection for higher transpiration rate and WUE would provide the required dividends of increased CGR while increasing WUE. In other words, any selection for WUE alone may not have any relevance in most cases. Fig. 3 clearly illustrates the lack of any relationship between WUE and total biomass among a number of rice germplasm accessions, especially when genotypes with large variations in leaf area (and hence in total transpiration) are included in the study.

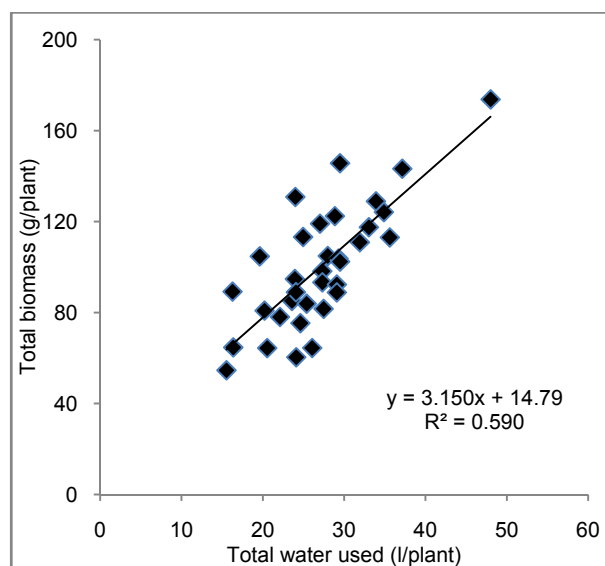


Figure 2. Relationship between total biomass and total water used by the canopy among diverse rice germplasm accessions

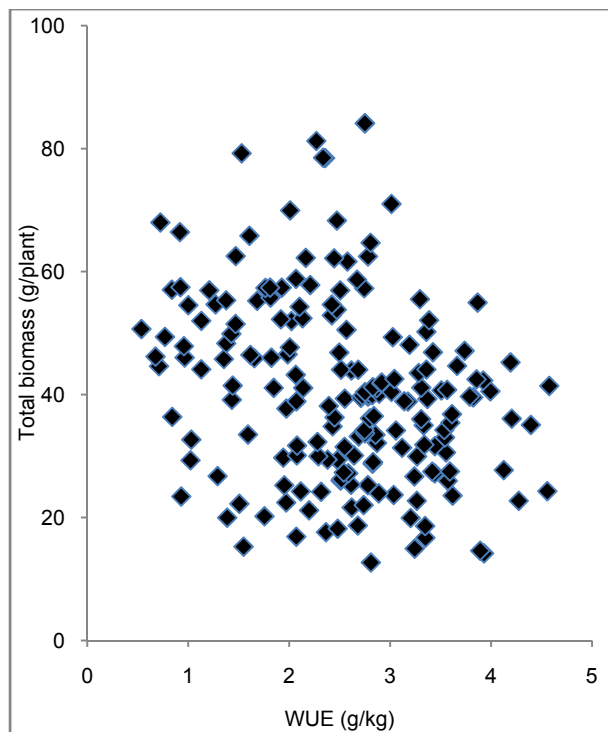


Figure 3. Relationship between total biomass and WUE among diverse rice germplasm accessions

In other words, if the variability in leaf area and total transpiration are large, assessing the relationship between WUE and total dry matter (TDM) would be futile.

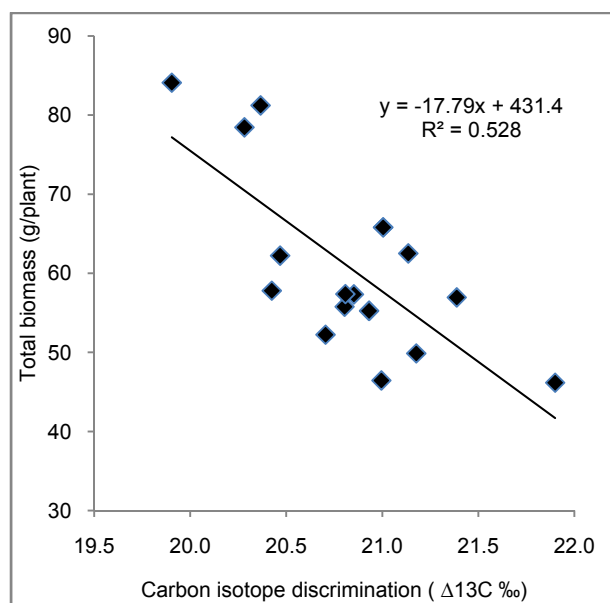


Figure 4. Relationship between total biomass and $\Delta^{13}\text{C}$, a surrogate for WUE and among genotypes with comparable leaf area

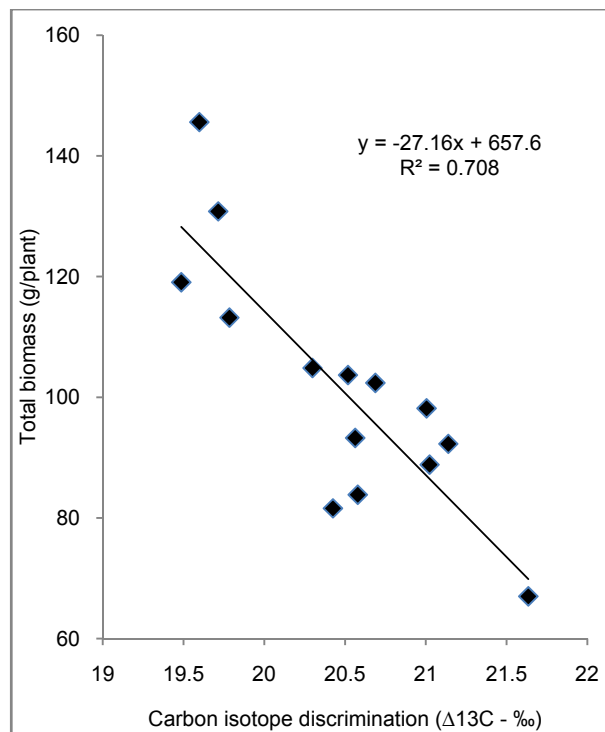


Figure 4b. Relationship between total biomass and $\Delta^{13}\text{C}$, a surrogate for WUE among genotypes with comparable total transpiration

On the other hand, when the variation in leaf area is smaller, that is, when the genotypes of similar leaf area are compared, a strong relationship between TDM and $\Delta^{13}\text{C}$ emerged (Fig. 4A).

Similarly, genotypes with comparable total transpiration also revealed a significant relationship between $\Delta^{13}\text{C}$ and total TDM (Fig. 4B)

These results suggest that undermining the importance of WUE as a trait influencing growth rate is not a scientific argument. It is evident that selecting for high WUE as an independent trait has relevance only when simultaneous selection of high canopy cover (leaf area) and transpiration are selected simultaneously.

This concept was examined from another angle. Though the leaf area was strongly associated with biomass accumulation, the association was weak or absent when genotypes with lesser differences in leaf area were compared (Fig. 5A and 5C). We computed the water productivity factor based on leaf area and WUE, by multiplying leaf area with WUE ($\text{WUE} \times \text{LA}$) and compared with the total biomass accumulation and hence CGR. A strong regression between water productivity estimate and total biomass provided a further confirmation on the importance of WUE as a trait contributing for CGR (Fig. 5B and 5D).

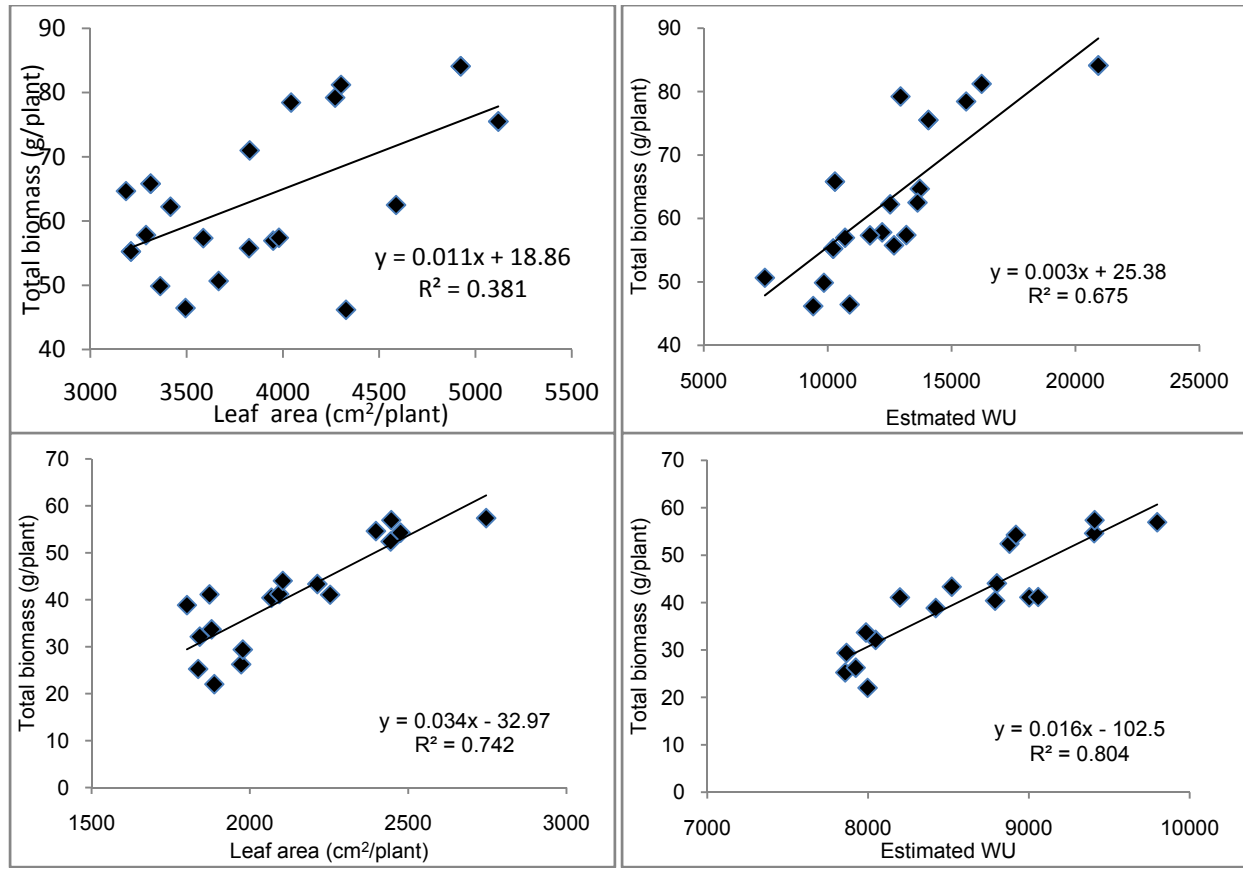


Figure 5. Illustration of the dependence between total biomass and leaf area among similar leaf area types [A with high) and C (low leaf area)]. The water productivity was computed by multiplying WUE with leaf area (estimated water use) and its association with total biomass was examined (B and D)

These results clearly emphasize that selection for both canopy cover and WUE has relevance. High WUE in the background of moderate to high leaf area will strongly contribute to improved crop growth rate.

Transpiration rate is strongly linked with WUE

Though total transpiration is determined by the transpirational surface area, and rate of transpiration, WUE seems to be tightly linked with the rate of transpiration and the negative relationship has evolved as a significant strategy to conserve water under natural conditions (Fig. 6). Such water conservation types, often referred to as the “Conductance types”, show a strong negative relationship between WUE and mean transpiration rate (Udayakumar et al 1998; Sheshshayee et al 2003).

However, water conservation need not be the only strategy for enhancing WUE, even under water limited conditions. It is also possible that carbon assimilatory capacity could also significantly contribute to the

variations in WUE. Such types would display no relationship or at best only a weak relationship between WUE and mean transpiration rate (Fig. 7).

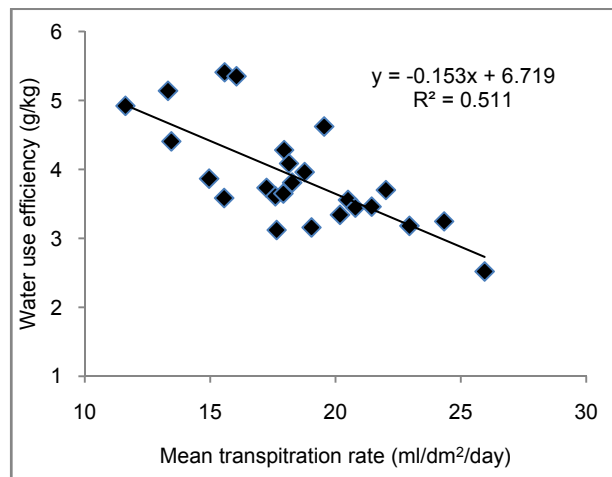


Figure 6. Relationship between WUE and mean transpiration rate among rice genotypes

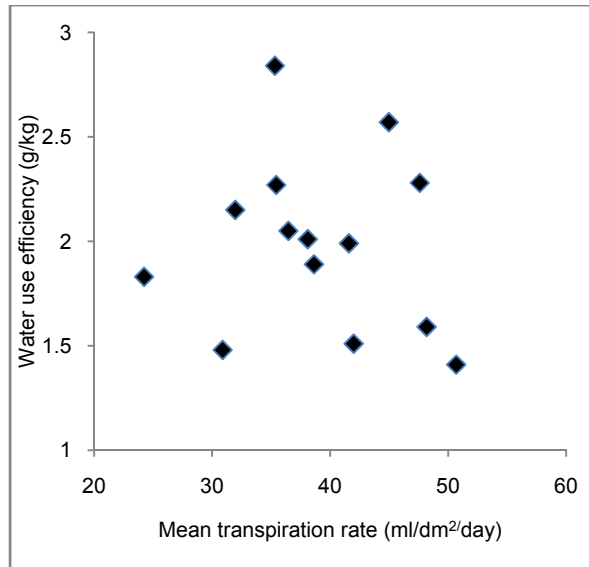


Figure 7. Relationship between water use efficiency and mean transpiration rate among a few contrasting groundnut genotypes.

The lines where WUE do not have a strong association with transpiration rate would have higher WUE by virtue of superior chloroplast capacity. In one of our earlier studies we demonstrated that by examining the relationship between WUE and transpiration rate, there is a possibility of identifying genotypes where WUE is independent of transpiration rate or where WUE is governed by the chloroplast capacity (Ashok et al 1995).

How to identify genotypes where transpiration rate and WUE have a weak association?

It is well established that at a given vapor pressure deficit (VPD), differences in WUE is influenced by the differences in the partial pressure of CO₂ in the intercellular spaces (Pi). WUE would be high at low Pi and vice-versa. Thus, factors that govern differences in Pi would also control the differences in WUE. Stomatal conductance (g_s) as well as the overall chloroplast capacity (g_m), control the differences in Pi and hence WUE. It is always desirable to identify genotypes that have higher WUE (i.e., low Pi), by virtue of superior chloroplast capacity. In such types, referred to as the "Capacity types", selection for high WUE does not associate with reduced biomass, because in these capacity types the dependence between WUE and transpiration rate is weak and hence selection for higher WUE does not associate with reduced photosynthetic rate. The following flow chart explains the relevance of capacity types.

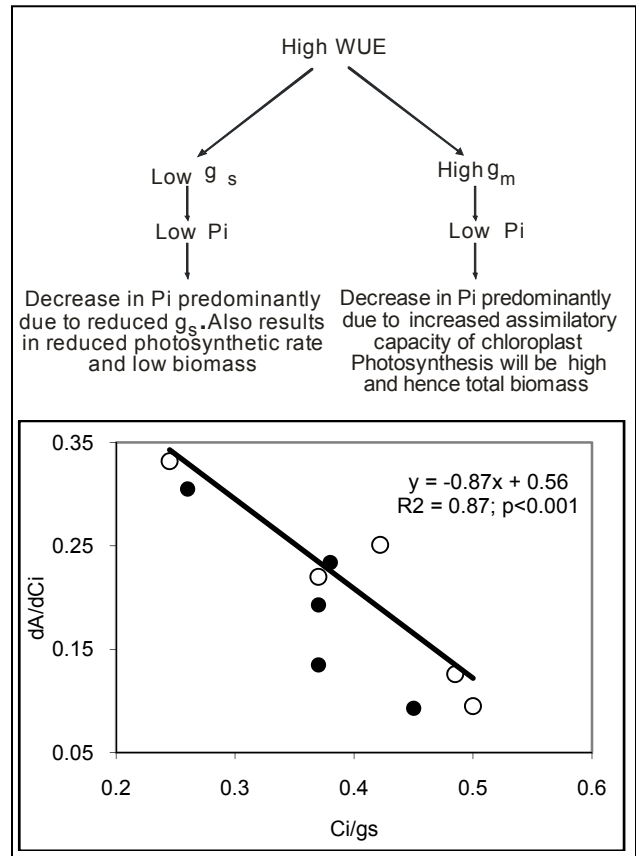


Figure 8. Relationship between the initial slope of CO₂ response curve (dA/dCi) and ratio of Ci to g_s. Note: dA/dCi is often considered as a good reflection of carboxylation capacity (Source: Bindumadhava et al 2005)

From this background, it is apparent that identification of high WUE genotypes where the regulation of Pi comes from the chloroplast capacity is most relevant. In such types, the Pi will be low at a given stomatal conductance (g_s) and the relationship between WUE and transpiration rate will not be negative.

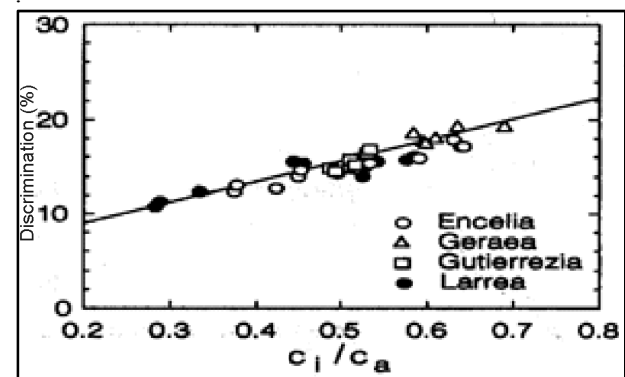


Figure 9. Relationship between Pi and Δ¹³C (Source: Hubick et al 1984)

These genotypes will have higher WUE despite a relatively high transpiration rate and hence can maintain higher net assimilation rate (NAR). This signifies the importance of identifying genotypes with higher chloroplast capacity (g_m). Unlike stomatal conductance, assessing variability in chloroplast capacity and the entire mesophyll efficiency is quite difficult. Other indirect methods, however, are often used. The initial slope of a CO_2 response curve (dA/dC_i) is often considered as an effective reflection of the carboxylation efficiency and hence mesophyll efficiency (Caemerrer and Farquhar 1981). We provided a simpler option based on gas exchange measurements, to assess the mesophyll efficiency. The intercellular CO_2 concentration (C_i) is a function of CO_2 supply by diffusion through stomata and assimilation of substrate CO_2 by all metabolic activities in chloroplast. Thus, variations in C_i at a given stomatal conductance (C_i/g_s) should be a rapid estimate of chloroplast capacity (Sheshshayee et al 1995). We have demonstrated the utility of C_i/g_s ratio as an accurate estimate of chloroplast capacity in several crop species (Krishnaprasad et al 1995) (Fig. 8). While carbon isotope discrimination has been well proven to be a reflection of C_i (Fig. 9), we provided experimental evidence for oxygen isotope enrichment to be a reflection of g_s (Fig. 10). Thus, the stable isotope ratios of carbon and oxygen ($\Delta^{13}C/\delta^{18}O$) was hypothesized to be a time integrated estimate of the C_i/g_s ratio and hence chloroplast capacity. Experiments using contrasting genotypes of different species indicated that $\Delta^{13}C/\delta^{18}O$ is in fact an accurate estimate of chloroplast capacity on a time integrated scale (Bindumadhava et al 2006). We have shown that $\Delta^{13}C/\delta^{18}O$ ratio correlated with other estimates of chloroplast capacity such as the initial slope of CO_2 response curve (dA/dC_i) (Fig. 11).

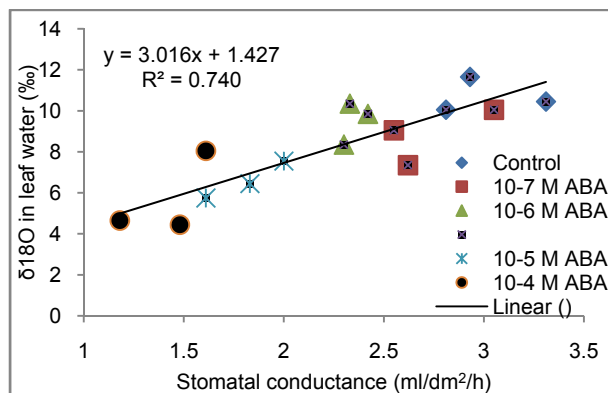


Figure 10. Relationship between oxygen isotope enrichment ($\delta^{18}O$) and stomatal conductance in rice. Leaf stomatal conductance was altered by providing different concentrations of ABA through the leaf petiole (Source: Sheshshayee et al 2005)

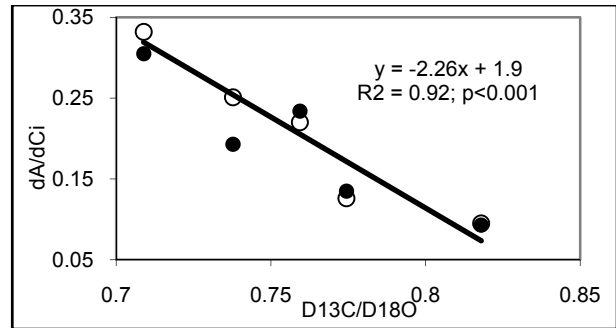


Figure 11. Relationship between the dA/dC_i and dual isotope ratio among contrasting genotypes.

The foregoing discussion clearly demonstrates the relevance of WUE as an extremely relevant trait to sustain productivity under water limited conditions. Further, the advantage of WUE is fully exploited when the genotype has adequate canopy cover. Furthermore, WUE has a much greater impact on growth when the differences in WUE are independent of transpiration rate. Therefore, selection for high canopy cover, transpiration rate and WUE should be the strategy to exploit the relevance of WUE in sustaining growth and saving water.

Water mining is important to sustain growth under semi-irrigated aerobic conditions

Root traits through mining water from deeper soil profiles can effectively extract water to support the evaporative demand of the canopy. Effective water mining is essential to maintain positive turgor and hence result in the maintenance of positive carbon gain. Several experiments conducted at our center and elsewhere have clearly demonstrated the relevance of root traits in sustaining growth rate, especially under water limited conditions (Fig. 12).

Despite the unequivocal agreement on the relevance of roots as potential drought adaptive traits, assessment of genetic variability in root traits has been one of the most challenging tasks. Phenotyping approaches for measuring root traits include growing plants in pipes, hydroponic conditions, or in agar plates. Certain imaging techniques have also been adopted for the determination of root growth. These techniques have certain important limitations that restrict their adoption for large scale phenotyping. We developed a novel approach to grow plants in specially constructed root structures - tanks of convenient size (Sheshshayee et al 2011). The soil in these raised root study structures is filled and compacted to mimic the natural field conditions. The greatest advantage of this approach is the possibility of maintaining plant population exactly as that in the field. In this condition, the interplant competition which significantly contributes to the phenotypic expression, can be effectively determined.

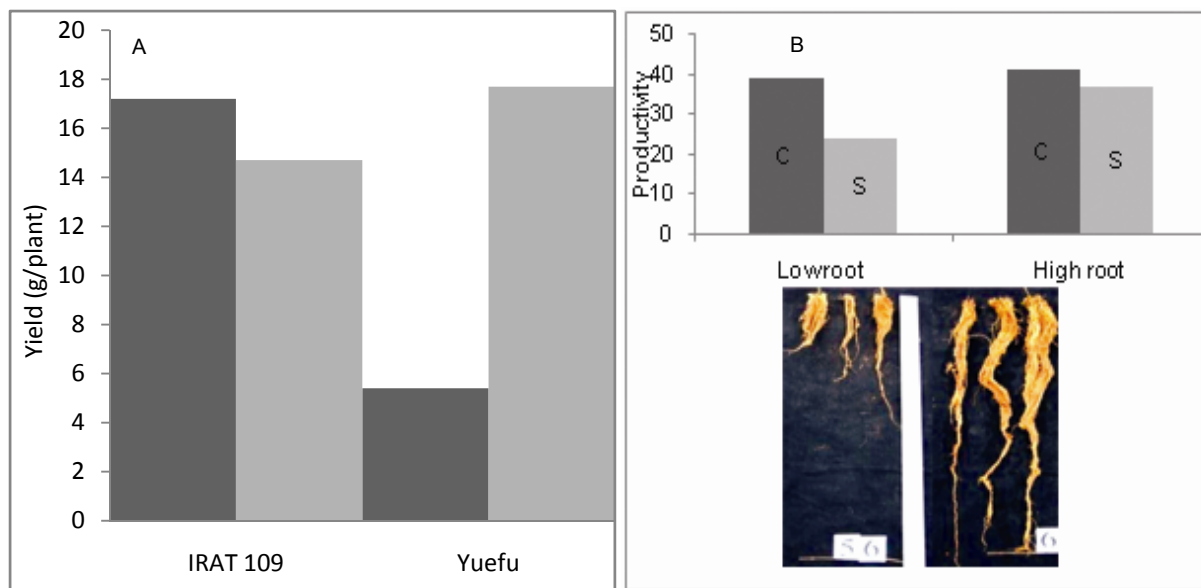


Figure 12. Relevance of root traits established in sustaining productivity under water limited conditions: A = re-drawn from Li et al 2005; B = re-drawn from Mohankumar 2011

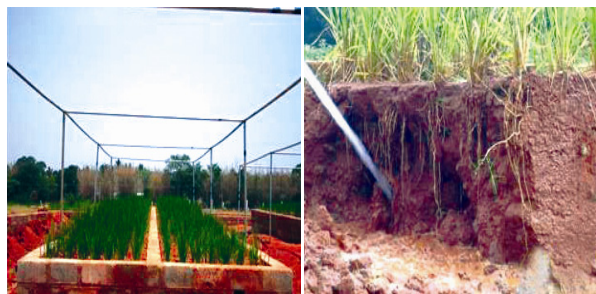


Figure 13. Root study structures for examining the root traits under natural conditions.

Thus, this approach represents one of the most appropriate phenotyping strategies for assessing differences in root traits. Typically, a root structure for the determination of genetic variability in root traits of rice will measure 1.8 m long, 1.5 m tall and 3.0 m wide (Fig. 13). The side walls can be easily dismantled at the end of the experiment and the soil washed off the roots using a strong jet of water.

Oxygen isotope enrichment as a surrogate for root traits

In most plant species, the total biomass accumulated is a function of the total water used through transpiration. Total transpiration is further a function of the evaporating surface area of the canopy and the extent of root development to supply water to match the evaporative demand. Hence, transpiration at a given leaf area must be related to root biomass and hence a good indicator of root traits.

We had earlier shown that the oxygen isotope enrichment ($\Delta^{18}\text{O}$) is an accurate surrogate for transpiration rate (Fig. 14, Sheshshatee et al 2005). Oxygen isotope enrichment values at a given leaf area was found to be strongly correlated with root biomass among rice accessions (Fig. 15). Being high throughput and very accurate, stable isotope ratio is a very useful approach for the determination of root traits in plants. This approach was effectively used for the determination of genetic variability in root traits among a large set of diverse germplasm accessions. A significant genetic variability was noticed among the germplasm accessions (Fig. 16 and 17) and the variation was normally distributed around the mean indicating the polygenic control of root traits.

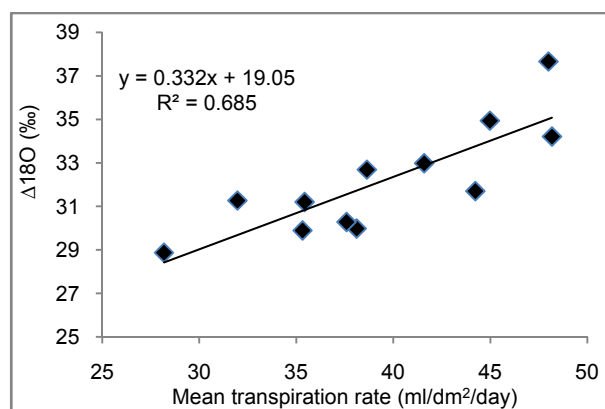


Figure 14. Relationship between oxygen isotope enrichment ($\Delta^{18}\text{O}$) and transpiration rate in rice genotypes. (From Sheshshatee et al 2005)

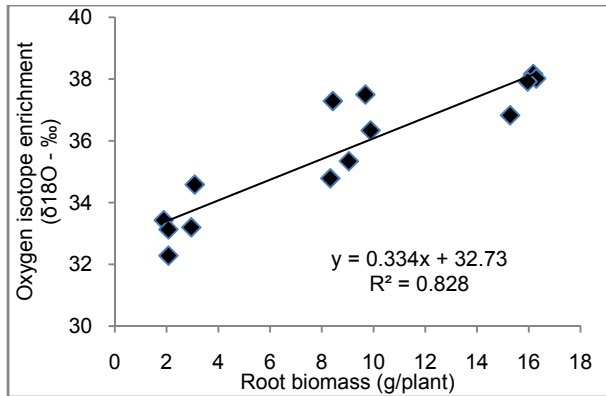


Figure 15. Oxygen isotope enrichment accurately reflects root biomass in rice

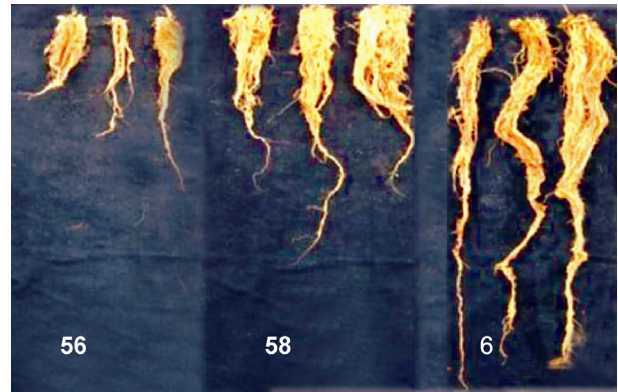


Figure 17. Representative variations in root architecture among rice germplasm

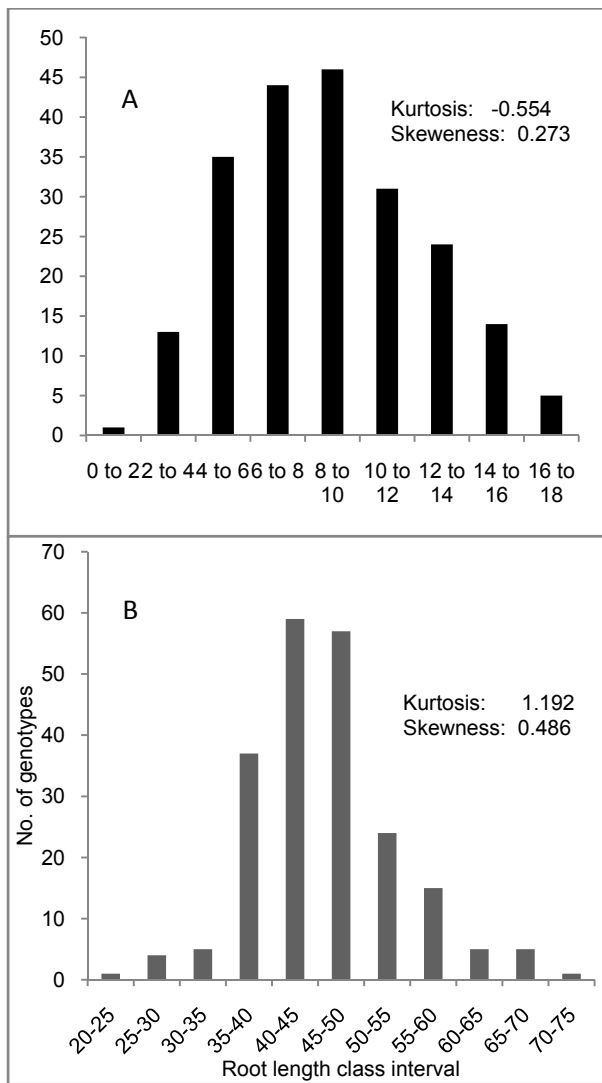


Figure 16. Genetic variability in root biomass (A) and root length (B) normally distributed among a set of diverse germplasm accessions of rice

Deep root traits significantly enhance the extraction of water from deeper layers and support the evaporative demand of the canopy. This effective water uptake though results in the maintenance of higher leaf tissue water status, would also be responsible for higher transpiration rates. Thus, high root biomass or deeper roots would have reduced WUE (high $\Delta^{13}\text{C}$).

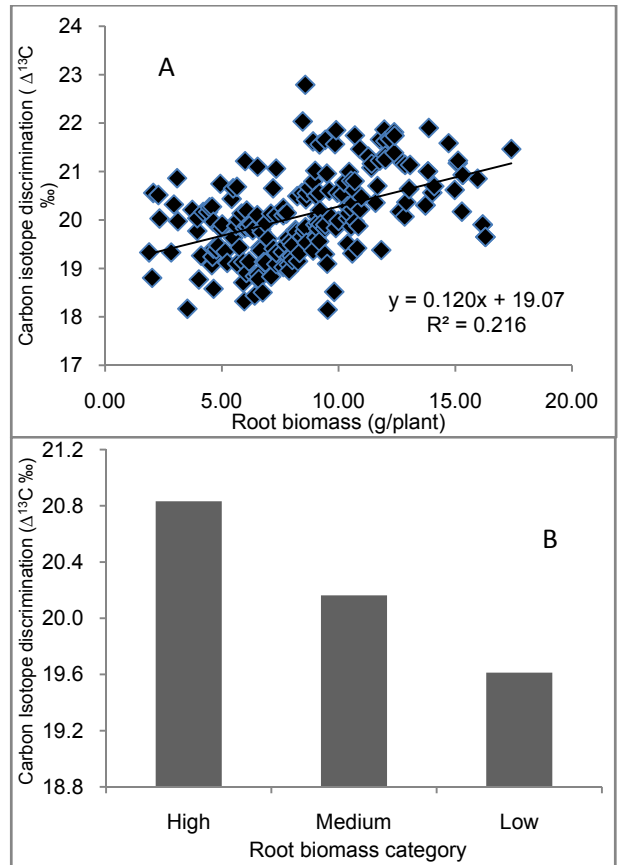


Figure 18. Relationship between $\Delta^{13}\text{C}$ and root biomass among rice germplasm accessions (A) and the differences in $\Delta^{13}\text{C}$ among accessions differing in root biomass (B).

The results (Fig. 18) provide the proof that high root types indeed have lower WUE. This variation in WUE caused by root traits appears to be a phenomenon associated with water extraction. However, the effective use of water would be possible only when this extra water extracted is efficiently used for biomass production. Therefore, it becomes essential to combine root traits with superior WUE if the advantages of both these traits are to be exploited. Only when high root traits are associated with greater WUE, the relevance of root traits in maintaining positive carbon gain would be exemplified.

Trait introgression to achieve greater growth rate and productivity

An attempt was made to introgress root traits with WUE by identifying the respective traits donor lines. By precise phenotyping of diverse germplasm accessions, lines with superior root characters and WUE were identified. The root donor line (IET15963) was crossed with a high WUE donor (Thanu) and the segregating progeny were screened for the trait introgression. KMP175 has emerged as a trait introgressed line which showed greater root biomass and higher WUE (Fig. 19). This trait introgressed line when grown under aerobic conditions outperformed all other checks (Fig. 20).

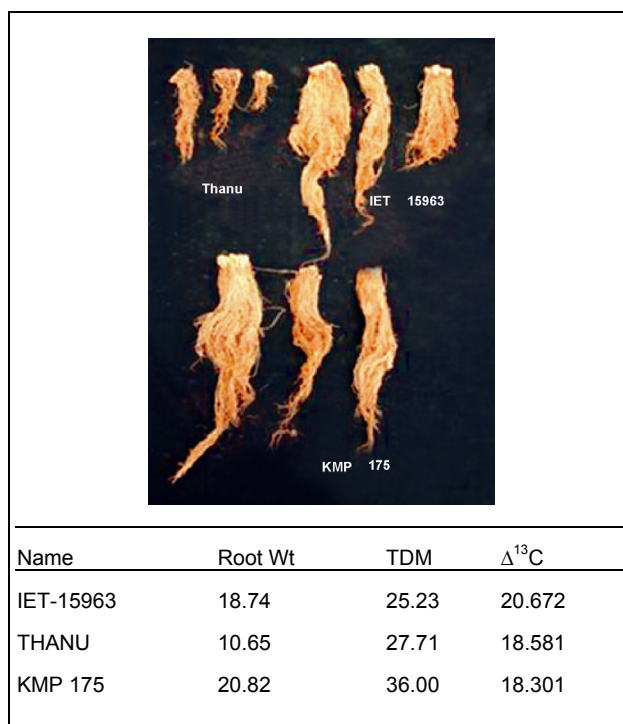


Figure 19. Variations in root traits and WUE among the trait donor lines and the trait introgressed line

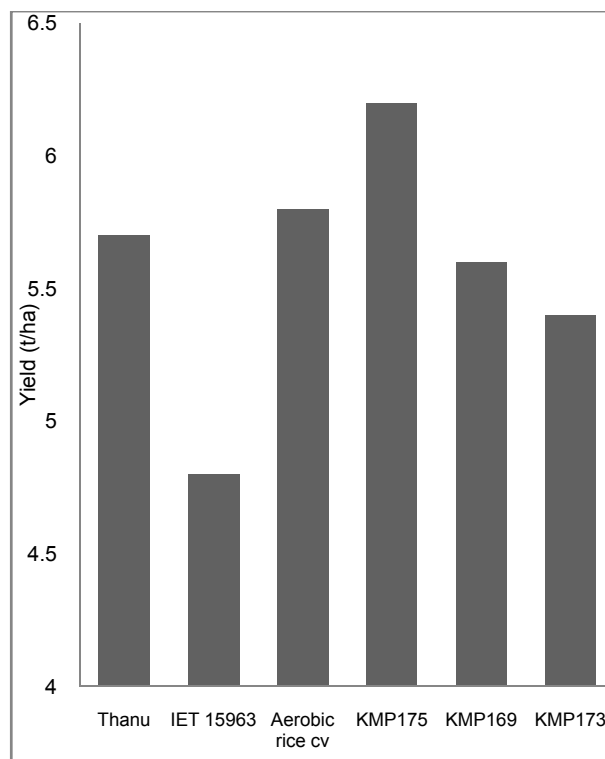


Figure 20. Yield performance of trait introgressed line compared with other cultivars recommended for aerobic cultivation

The results signify the relevance of both WUE and root traits in enhancing the productivity under water limited conditions. Further, it is clearly evident from these results that combining these drought adaptive traits has greater relevance than any of them individually.

Epicuticular waxes - a trait that imparts drought adaptation

Besides effective uptake of water and its efficient use for biomass production, water conservation also plays an extremely important role in the overall water productivity of the plant. Epicuticular waxes form a thin hydrophobic film on the leaf surface and have long been known for their role in reducing the non-stomatal water loss. Waxes reflect radiation and hence can significantly reduce the heat load on leaves which in turn leads to the maintenance of lower VPD and hence the plants would have significantly reduced transpiration at a given stomatal conductance. The relevance of epicuticular waxes in avoiding the non-stomatal water loss was assessed in a diverse set of rice germplasm accessions. A simple approach of extracting the epicuticular waxes by dipping the leaves in chloroform for 5 sec was standardized.

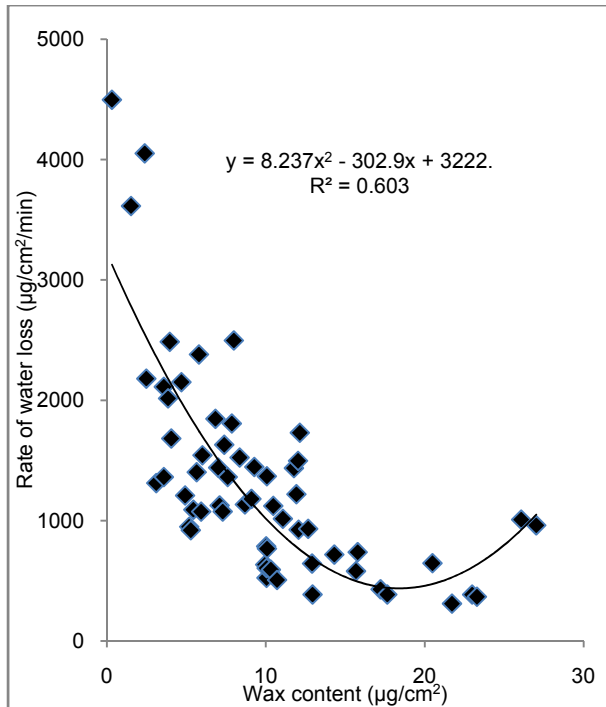


Figure 21. Relationship between non-stomatal water loss and epicuticular wax load among rice accessions

A significant genetic variability was noticed among the rice germplasm (Fig. 22) indicating the possibility of exploiting it for further trait improvement.

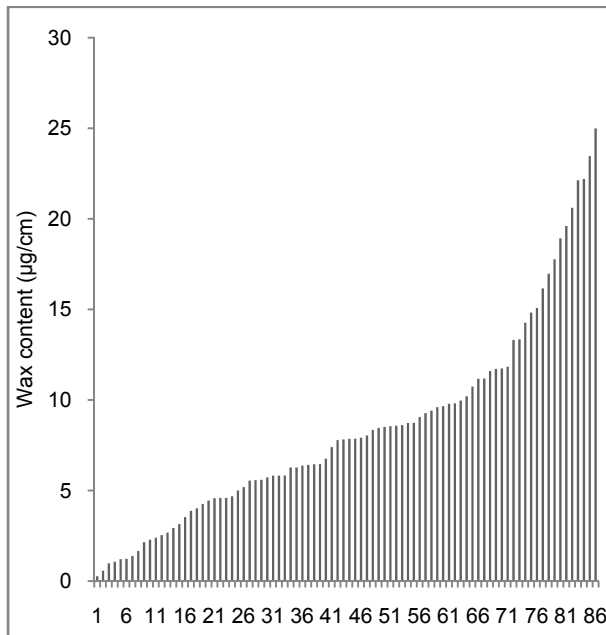


Figure 22. Genetic variability in epicuticular wax content among rice germplasm accessions

Conclusion

In summary, our results show that WUE, besides effective use of water is an important trait to improve productivity of rice cultivars grown under semi-irrigated aerobic cultivation. Selection for these two important traits in addition to the higher epicuticular wax loads not only improves water relations but also growth rate. In addition, mechanisms associated with cellular level tolerance are important especially for improved spikelet fertility. Despite an inverse relationship between WUE and root traits, introgressing these two traits is relevant. This signifies the need to identify robust markers and QTLs associated with these traits.

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